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FISHERIES MANAGEMENT REPORT No. 90

1988



Province of British Columbia
Ministry of Environment and Parks

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THE EARLY GROWTH OF KOKANEE (Oncorhynchus nerka) FRY
IN RELATION TO RATION

by

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Fisheries Management Report No. 90
1988

Province of British Columbia
Ministry of Environment and Parks

Canadian Cataloguing in Publication Data

Main entry under title:

The Early growth of kokanee (*Oncorhynchus nerka*)
fry in relation to ration

(Fisheries management report, ISSN 0705-5390 ; no.
90)

ISBN 0-7726-0783-4

I. Sockeye salmon - Growth. I. Johnston, N. T.
II. British Columbia. Ministry of Environment and
Parks. III. Series: Fisheries management report
(British Columbia. Fisheries Branch) ; no. 90.

QL638.S2E27 1988 639.3'755 C88-092051-3

ABSTRACT

Johnston, N.T., C.J. Perrin, H.A. Andrusak, and E.A. Parkinson. 1988. The Early Growth of Kokanee (Oncorhynchus nerka) Fry in Relation to Ration. Fisheries Management Report No. 90, 13 p.

The growth rates of newly-emerged kokanee fry reared at ambient conditions of temperature and food in net pens in the West Arm of Kootenay Lake were 3.5 to 4.9% per day during two 20-day experiments. Kokanee fry reared under the same regime of temperature at a series of fixed rations (4 to 32% body weight.d⁻¹) at the Meadow Creek hatchery had maximum daily growth rates of 2.4% at excess rations. The growth of hatchery-reared fry generally increased with increasing rations, except that fry did not gain weight at the 4% ration. The early growth of kokanee fry in the West Arm did not appear to be adversely affected by recent decreases in nutrient loadings to the lake.

ACKNOWLEDGEMENTS

We thank Kerry Andrusak and Les Fleck for their able assistance. This project was supported by funds from the Habitat Conservation Foundation.



INTRODUCTION

The growth of *Oncorhynchus nerka* fry may frequently be limited by food availability. Brett (1971a) noted that the observed growth rates of *O. nerka* fry were much lower than those possible at satiation rations. A strong positive relationship between fry growth and zooplankton biomass was shown for Babine Lake sockeye (Johnson 1961). The growth response of sockeye fry to lake fertilization (Hyatt and Stockner 1985) further suggests food limitation of growth rates. The diel vertical migrations of *O. nerka* fry (Narver 1970) may constrain their growth by limiting foraging to brief periods (Levy 1987).

Because fry mortality is size-selective (West and Larkin 1987), changes in food availability may influence survival by altering growth rates; low food availability is not likely to kill fry directly, as was evident in starvation experiments (Bilton and Robins 1971). The early growth of *O. nerka* fry has been little studied (e.g. Biette and Geen 1980; Rieman 1981), although the growth of larger juvenile sockeye in relation to ration and temperature has been extensively documented in laboratory experiments (Brett et al. 1969; Shelbourn et al. 1973; Brett and Shelbourn 1975). However, small differences in initial growth rates may be important in setting up size differences that could lead to survival differences.

We have attempted to assess whether the early growth of a natural population of kokanee (nonanadromous *O. nerka*) was food limited. We determined the growth rates of newly-emerged kokanee fry in their natural environment by pen-rearing experiments, and compared the observed growth to that of fish reared at known rations under the same temperature regimes in hatchery troughs. The goal of the work was to assess the effects of altered limnological conditions in Kootenay Lake (Northcote 1973; Daley et al. 1981) on the early growth of the West Arm stock, which has undergone catastrophic declines in adult returns simultaneously with decreased inputs of phosphorus to the main lake.

METHODS

Study Site

Kootenay Lake (Fig. 1) is a large (389 km²), deep (z=107 m) lake in southeastern British Columbia. The limnology of the lake was described by Northcote (1973) and Daley et al. (1981), while its fisheries were described by Northcote (1973). During the 1960's, phosphorus discharges from a fertilizer plant on a major inflow resulted in cultural eutrophication of the lake (Northcote 1973). Pollution abatement and the construction of a storage reservoir on the inflow greatly reduced phosphorus inputs by the mid-1970's (Daley et al. 1981). During this period, a large and economically important sport fishery for kokanee

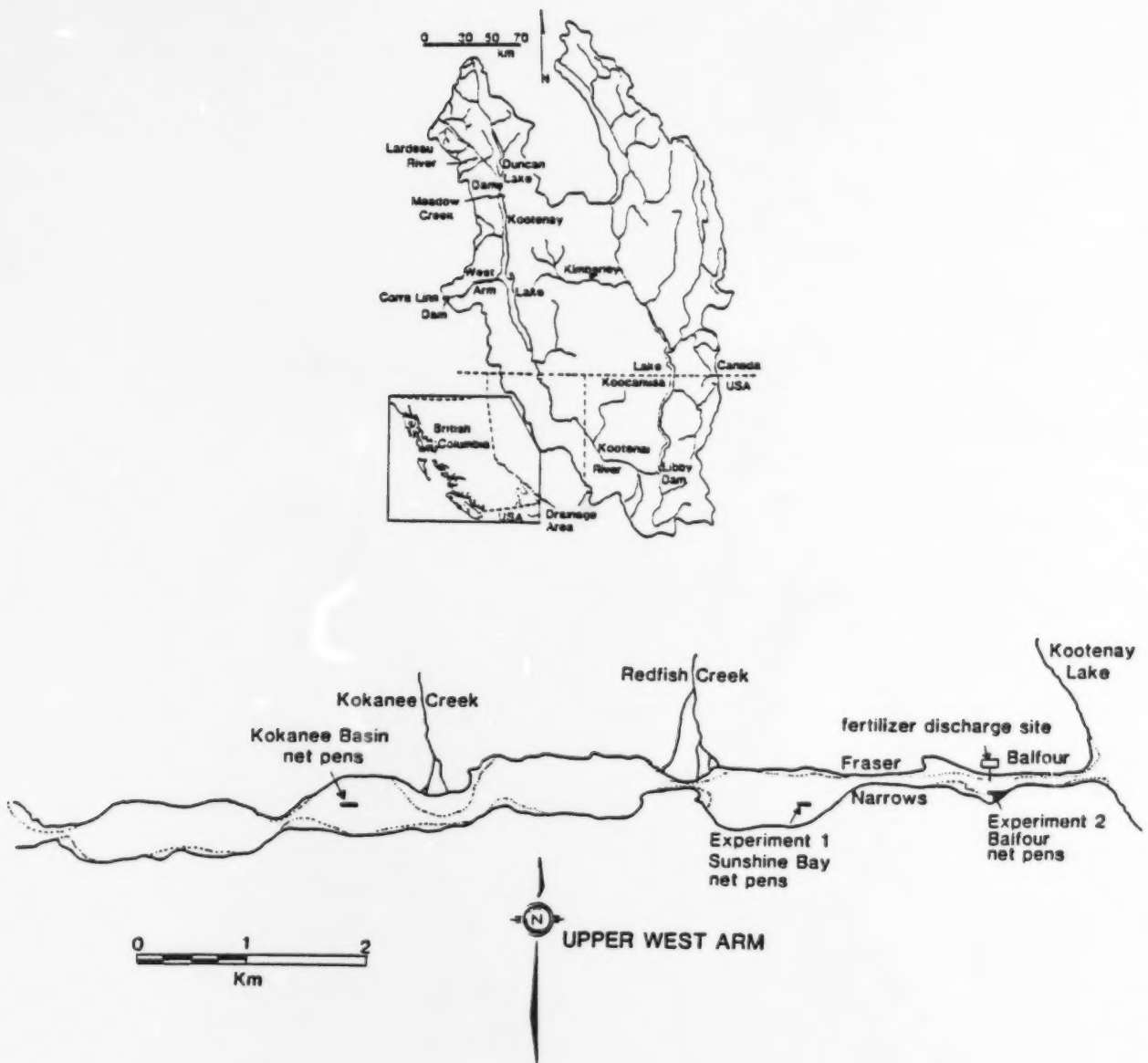


Figure 1. Kootenay Lake, showing the study sites.

developed, especially on the West Arm. The West Arm kokanee fishery has subsequently collapsed (Andrusak 1981). A variety of factors, including overfishing, poor egg-to-fry survival, and reduced fry survival may be involved in the decline of the West Arm kokanee fishery. However, closure of the fishery, improved fry production from spawning channels, and limited stocking of fry have not increased recruitment to the fishable population.

The main lake discharges into the West Arm over a shallow sill. The West Arm itself consists of a series of relatively shallow basins connected by shallow, riverine narrows. Water velocity at the narrows is about 1 m.s^{-1} , but is less than 0.1 m.s^{-1} in the basins. The water column is well mixed and is not thermally stratified in summer: the variation in temperature over the water column or among the three uppermost basins is less than 0.2° C . The zooplankton community is an outwash community from the epilimnion of the main lake. The zooplankton of the main lake was described in Zyblut (1970), and is dominated by the copepods Cyclops bicuspidatus thomasi and Diaptomus ashlandi and by the mysid Mysis relicta, which was introduced in 1949 (Sparrow et al. 1964), and became established at high densities in the late 1960's. The kokanee comprise three distinct stocks (Vernon 1957) which spawn in streams flowing into the three separate arms of the lake.

Rearing Experiments

The experiments compared the growth of newly-emerged kokanee fry reared in net pens in their natural environment against the growth of fry of the same origin that were reared in hatchery troughs under the same temperature regime at a series of fixed rations. The experimental design was a one-way nested analysis of variance, with replicate pens or troughs of fish nested within the "ration" treatments. Two separate growth comparisons were done utilizing early and late outmigrating fry from the Redfish Creek spawning channel (Fig. 1). In the first experiment, the growth of fry in net pens at two locations in the West Arm were compared to the growth of fry reared at the Meadow Creek hatchery at daily rations of 4, 8, 16, and 24% of their body weight (dry weight-dry weight basis). The rations were intended to cover the range from starvation to excess food, based on data for larger fry (Brett and Shelbourn 1975). In the second experiment, ration levels for the hatchery-reared fish were increased to 16%, 32% and excess food.

Downstream migrating fry were collected with drift nets from the Redfish Creek spawning channel the night prior to the start of each experiment, held overnight, and transported to the rearing sites in 25 L coolers the next day. Approximately 60 fish were placed in each pen or trough. All fry used in each of the two experiments came from a single collection. At the Meadow Creek hatchery, fry were reared in 4.8 m aluminum starter troughs divided in half by an aluminum screen. Each half trough was used as a cell to which ration treatments were randomly allocated,

subject to the constraint that higher rations must be located downstream of lower rations to minimize the drifting of excess food between cells. Each ration level was replicated in two treatment cells. Water depth was 10 cm and current velocity was 1 cm.s^{-1} at an average flow rate of 0.5 L.s^{-1} . Since the spring water supply was cooler than the West Arm, heaters in the water supply header tank were used to match water temperatures in the hatchery to that in the West Arm. Temperatures were continuously monitored in the hatchery header tank with a Weksler thermograph and in Kokanee Basin of the West Arm with a Ryan J-90 submersible thermograph. The thermographs were calibrated weekly. The start of the hatchery experiments lagged the pen rearing experiments by several days to allow hatchery temperatures to follow field temperatures. A 14 h light, 10 h dark cycle was maintained. Plywood covers were placed over half of each treatment cell to provide both cover and an open area into which feed could be added.

Hatchery fry were initially provided with excess food (BioDietTM starter) until they were observed to start active feeding; active feeding occurred within 2 d. At that time, all food was removed from the troughs and the correct feeding regimes commenced. The day following the start of active feeding was considered the first day of the experiment. Food was added twice daily in equal amounts. At feeding time, water flow in the troughs was stopped and the food was added by hand over a half hour period. Water flow was restarted when no food remained or when feeding had stopped. Any uneaten food was removed. The amount of food added was adjusted daily for mortalities and at 10-12 d intervals for changes in fish weight. Wet to dry weight conversions of 0.22 and 0.785 were used for fish and food, respectively.

In each experiment, 4 replicate net pens were located at each of two sites in the West Arm to measure fry growth under ambient temperature and food conditions. The net pens were 1.2 X 1.2 m square and 3 m deep, and were constructed of 3 mm nylon mesh with weights at each corner. At each site, 4 pens were secured together about 5 m apart. The pens were covered with a plywood lid after day 10 of the first experiment and were cleaned weekly. The pens were located at Kokanee Basin and Sunshine Bay in the first experiment, and at Kokanee Basin and opposite Balfour in the second (Fig. 1). The water depths at the pens were about 10 m at Kokanee Basin and Sunshine Bay, and about 5 m at Balfour. Surface current speed was about 10 cm.s^{-1} at all sites. Each experiment started 24 h after fish were placed in the pens.

Zooplankton were collected within each of the pens at each site on three dates spanning both experiments by making a 3 m vertical haul using a $153 \mu\text{m}$ mesh conical plankton net having a mouth area of 0.057 m^2 . Three similar collections were also made outside the pens at the same time. Zooplankton samples were preserved in 5% formalin, subsampled by drawing 1 mL aliquots to

give total counts of several hundred organisms, and organisms identified and counted at 30-70 X magnification. Nauplii were not identified to species. Variance-to-mean ratios (Elliott 1977) of subsamples ($n=8$) drawn from the same sample indicated that all groups were randomly subsampled. Differences in zooplankton abundance inside and outside the pens were examined using a one-way analysis of variance.

The wet weights of fry were determined at the start of each experiment, at either 10 d or 12 d, and at 20 d by weighing 3 groups of 5 fry from each pen or trough. The fish subsample was removed prior to feeding, anaesthetized in a 2-phenoxyethanol solution and weighed to the nearest 0.01 g. Because of the small size of the fish, it was not possible to blot off water adhering to the fish without causing injury. A correction factor was determined on the final day of each experiment by weighing the fry as above, and then reweighing the same fish after killing them and carefully blotting excess water. The first experiment ran from May 8 to May 27 at the West Arm sites, and from May 12 to June 1 at Meadow Creek hatchery. The second experiment ran from May 29 to June 17 in the West Arm, and from June 1 to June 21 at Meadow Creek.

Fry weights at day 0, 10 and 20 were compared among treatments (ration level or lake location) using a nested analysis of variance with replicate pens or troughs nested within treatments; this analysis was done to confirm that initial weights were identical in all subgroups (troughs or pens) and that among subgroup differences were nonsignificant. Satterthwaite's approximation (Sokal and Rohlf 1981) was used, where appropriate, in testing among group differences. Tukey's test was used to compare means. Average instantaneous growth rates over first 20 d of feeding were calculated by least-squares fitting linear regressions to log transformed weight-at-time data, and were compared by analysis of covariance.

The diet of the pen-reared fry was obtained from stomach samples of 30 fry collected from each of the two sites at the end of each experiment. Fry were anaesthetized and preserved in 95% ethanol. Their stomachs anterior to the pyloric ceca were excised, the contents identified, enumerated under low magnification, and weighed to the nearest mg.

RESULTS

The specific growth rates of kokanee fry varied greatly among treatments (Table 1). The initial weights of fry did not differ among treatments in either experiment (ANOVA, $p>.05$), but final weights differed considerably (Table 1). There were no differences among subgroups (troughs or pens) within treatments in either experiment (ANOVA, $p>.05$). Temperature regimes were similar at the hatchery and in the West Arm (Fig. 2). During the first experiment, the ambient temperature increased from 7 to

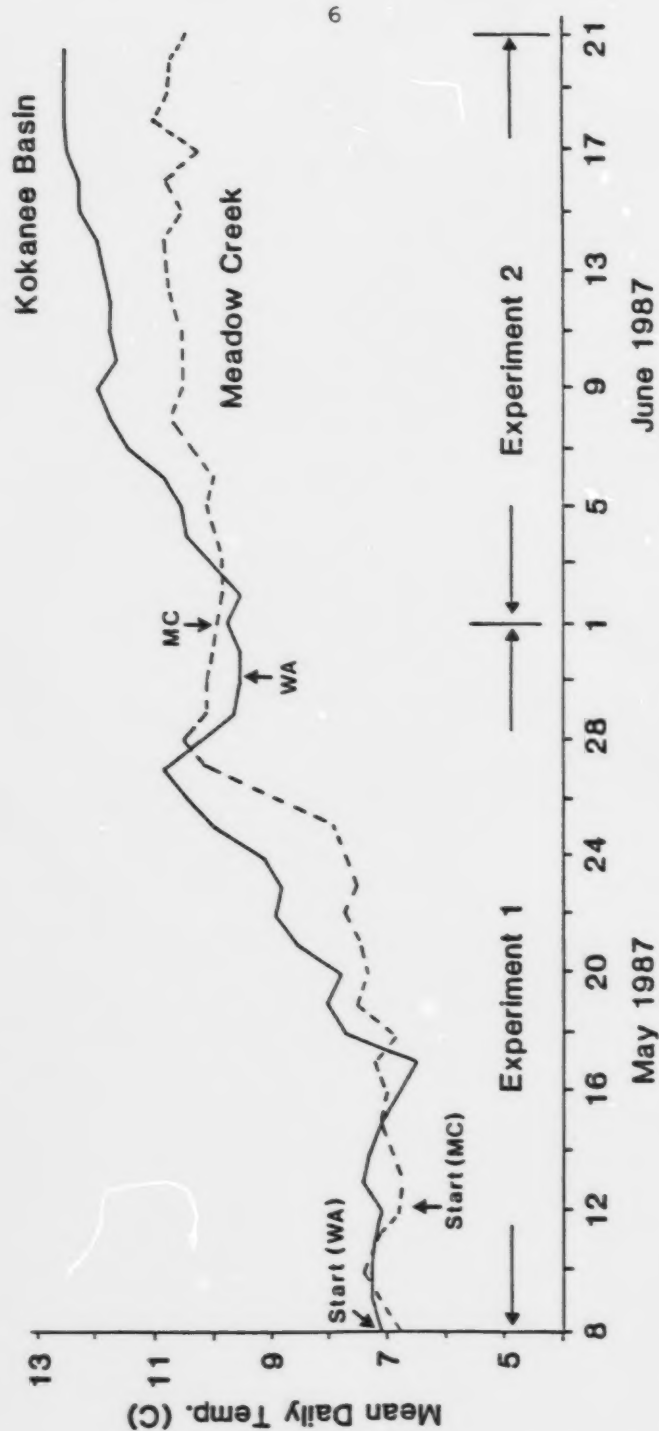


Figure 2. Temperatures at West Arm net pens and in hatchery troughs during the rearing experiments. Note that the start of the experiment at Meadow Creek lagged that in the West Arm by several days to facilitate temperature adjustments at the hatchery.

10.5° C, and averaged 8.1° C at both sites. Temperatures rose from 10 to 13° C during the second experiment and averaged about 10.5° C at the hatchery and 11.1° C in the West Arm. Fry mortality occurred at all treatments, primarily from the handling associated with weight measurements, but was generally low (Table 2).

Table 1. Initial and final wet weights (mean $\pm$ SE) of groups of five kokanee fry, and specific growth rates from least squares fit to log-transformed size-at-time data.

Expt.	Treatment	Initial Wt. (g.5 fish)	20 Day Wt. (g.5 fish)	Specific Growth Rate (%.d ⁻¹)
1	4% ration	0.54 $\pm$ 0.029	0.54 $\pm$ 0.027	-0.42 $\pm$ 4.31 ^a
1	8% ration	0.53 $\pm$ 0.025	0.73 $\pm$ 0.042	1.61 $\pm$ 0.37 ^{ab}
1	16% ration	0.55 $\pm$ 0.036	0.74 $\pm$ 0.027	1.52 $\pm$ 0.39 ^{ab}
1	24% ration	0.52 $\pm$ 0.044	0.80 $\pm$ 0.029	2.19 $\pm$ 0.42 ^{bc}
1	Sunshine Bay	0.58 $\pm$ 0.084	1.21 $\pm$ 0.049	3.46 $\pm$ 0.32 ^{cd}
1	Kokanee Basin	0.54 $\pm$ 0.055	1.15 $\pm$ 0.018	4.83 $\pm$ 0.45 ^d
2	16% ration	0.51 $\pm$ 0.047	0.62 $\pm$ 0.029	0.95 $\pm$ 0.37 ^a
2	32% ration	0.52 $\pm$ 0.028	0.73 $\pm$ 0.027	1.59 $\pm$ 0.35 ^{ab}
2	excess ration	0.45 $\pm$ 0.018	0.74 $\pm$ 0.031	2.39 $\pm$ 0.27 ^b
2	Balfour	0.50 $\pm$ 0.019	1.26 $\pm$ 0.020	4.50 $\pm$ 0.21 ^c
2	Kokanee Basin	0.46 $\pm$ 0.019	1.24 $\pm$ 0.032	4.88 $\pm$ 0.23 ^c

a, b, c, d indicate growth rates that do not differ ($p > 0.05$, Tukey's hsd test) within each experiment.

Table 2. Average numbers of fry alive in pens or troughs after weight determinations at days 0, 10 and 20.

Experiment 1:						
Day	4%	8%	16%	24%	Sunshine	Kokanee
0	60	60	60	60	57	53
10	57	58	57	58	31 ^a	37 ^a
20	44	48	50	44	29	35
Experiment 2:						
Day	16%	32%	excess	Balfour	Kokanee	
0	60	60	60	60	60	
10	59	58	59	55	56	
20	53	52	58	52	53	

^a losses of fry from pen rather than mortality.

Despite similar temperature regimes, kokanee fry reared under ambient conditions in the West Arm had higher growth rates than fry reared under high rations in the hatchery (Table 1). The growth rates of hatchery-reared fry generally increased with increasing rations. During the first experiment, however, fry reared at a daily ration of 4% of their body weight did not gain weight. Daily rations of 8-24% resulted in similar growth rates, the highest of which was comparable to the slower-growing pen-reared fry (Tukey test, $p > 0.05$). At the slightly higher temperatures of the second experiment, however, the growth rates of the pen-reared fry exceeded those of all hatchery-raised fry.

Zooplankton densities inside the net pens were consistently lower than those outside (Table 3), but the differences were not statistically significant (t-test, $p > 0.05$). The zooplankton community was dominated by the copepods Cyclops bicuspidatus and Diaptomus ashlandi which, together with unidentified nauplii, comprised more than 90% of the macroplankton numbers both inside and outside the pens. The cladocerans Diaphanosoma leuchtenbergianum and Bosmina sp. also occurred but were rare. The stomach contents of pen-reared fry consisted almost exclusively of copepods. Both Diaptomus and Cyclops were found in stomachs, but the condition of the specimens did not allow an accurate measure of their relative proportions. Mysis relicta juveniles and chironomids occurred rarely. Both weights and numbers of prey in stomachs increased from the first experiment to the second but consistent differences between the upstream and downstream sites did not occur (Table 4).

Table 3. Zooplankton abundances (mean $\pm$ SE) inside and outside net pens at sites in the West Arm of Kootenay Lake. Units of 1000.m⁻³.

Date	Kokanee Basin pens		Sunshine Bay/Balfour pens	
	Inside	Outside	Inside	Outside
08 May	9.8 $\pm$ 5.7	10.3 $\pm$ 7.4	15.9 $\pm$ 9.3	12.1 $\pm$ 8.6
27 May	41.7 $\pm$ 25.7	50.2 $\pm$ 35.5	30.4 $\pm$ 17.7	39.7 $\pm$ 28.1
17 June	34.4 $\pm$ 20.0	41.3 $\pm$ 29.6	29.0 $\pm$ 17.4	34.5 $\pm$ 24.5

Table 4. Average wet weight and number of prey organisms in the stomachs of kokanee fry collected from net pens in the West Arm of Kootenay Lake. SE in brackets.

	Wet Weight (mg)		No. Prey Items	
	Expt. 1	Expt. 2	Expt. 1	Expt. 2
Balfour/Sunshine Bay	3.0(0.2)	3.8(0.2)	11.7(0.9)	20.2(2.9)
Kokanee Basin	1.8(0.1)	3.4(0.2)	15.9(1.3)	34.1(4.2)

DISCUSSION

Our data suggest that the early growth of kokanee fry in the West Arm was not restricted by food availability, despite the changes in production in recent years documented by Daley *et al.* (1981). Comparison of the growth rates of the West Arm fry to those of fry reared at known rations allows an assessment of food availability in the West Arm. The early growth of kokanee fry under ambient conditions of food and temperature in net pens in the West Arm surpassed that of fry reared in the hatchery at the same temperatures and fed excess rations. The growth rates observed for early emigrating fry in the West Arm during the first experiment were comparable to those predicted for salmon fed at their growth-maximizing ration, while those of the later emigrating fry used in the second experiment were intermediate between the two predicted values (Table 5). The growth rates were also higher than those (<2.5%) observed at similar temperatures in pen rearing experiments at Pend Oreille Lake (Rieman 1981).

Table 5. Predicted specific growth rates (% $\cdot$ d⁻¹) of *O. nerka* fry at maximum rations.

Temperature ^a (° C)	Weight ^b (g)	Predicted		Observed Rate
		Brett and Shelbourn ^c	Stauffer ^d	
8.1	0.13	-	4.80	2.19
	0.16	-	4.47	3.46 - 4.83
10.5	0.13	4.26	6.35	2.39
11.1	0.16	4.16 ^e	6.29	4.50 - 4.88

^a arithmetic mean temperatures in experiments 1 and 2

^b geometric mean fry weights in experiments 1 and 2

^c extrapolated from Table 2 of Brett and Shelbourn (1975)

^d calculated from Stauffer (1973), as given in McLean (1979)

^e calculated at 10.5° C

However, the growth rates of hatchery-reared fry were considerably less than those of the pen-reared fry even at daily rations which exceeded the appetite of the fry during feeding bouts. Controlled studies with other fishes have similarly been unable to produce lab growth rates as high as those observed in nature (e.g. Laurence *et al.* 1979; Conover and Fleisher 1986).

Several factors may lower the growth of hatchery-reared kokanee fry. Continuous feeding results in higher growth than periodic feeding to satiation (Shelbourn *et al.* 1973). Since pen-reared fry could potentially feed throughout the day, while the hatchery fry were fed to satiation twice daily, higher growth would be expected for the pen-reared fry. The duration of periodic feeding bouts can also influence growth rates. Brett (1971b) suggested that a 60-min feeding period would satiate sockeye salmon, independently of size. We used approximately 30-min feeding periods, since most feeding activity ended within that period. The growth rates of the hatchery-reared fry were, however, considerably lower than those of slightly larger fry fed thrice daily for half hour periods at similar temperatures (Shelbourn *et al.* 1973). The nature of the diet can considerably influence growth rates of salmonids (Brett 1971c; Lemm and Hendrix 1981). In a comparison of numerous starter diets, BioDiet starter produced the highest growth in Atlantic salmon (Lemm and Hendrix 1981). Gross conversion efficiencies for artificial diets are typically 20 to 40% on a dry weight basis (Brett 1971c). However, gross conversion efficiencies for natural zooplankton are also high (about 25 to 30% at the temperatures in the West Arm, Biette and Geen 1980), so that major differences between zooplankton and BioDiet were not expected. Growth rates may also vary with particle size (Wankowski and Thorpe 1979). The range of prey sizes available in natural zooplankton may allow fry to select particles that maximize growth, which the more uniform particle size of the BioDiet starter might not permit. If data from Atlantic salmon fry can be applied to kokanee, a prey size of 0.75 mm would maximize growth. Small copepodites of this size are abundant in the West Arm zooplankton in late spring (N.T. Johnston, unpublished data) but particles of that size would not be common in the starter. Finally, kokanee fry feeding for the first time may more quickly learn to identify and capture prey when exposed continuously to live zooplankton than when periodically fed a dust-like starter chow.

The high growth rates of kokanee fry reared in pens in the surface waters of the West Arm suggest that conditions in the West Arm have remained favorable for growth despite reduced loadings of P to the Main Lake. Rearing conditions evidently remained favorable throughout the summer, as the mean size of fry in early October was 7.5 g (SE=0.5, n=23) (E.A. Parkinson, unpublished data). Thus, it is unlikely that food limitation of early growth was an important determinant of mortality throughout the first summer of life. If the hatchery growth data at known rations are correct, the pen growth rates imply an available

ration of at least 25% per day in the pens. Such food availability raises the possibility of rearing kokanee fry without supplemental feeding.

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